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New eco-morphological-behavioural approach of the chinchilla rats in the pre-Andean foothills of the Monte Desert (Argentina)

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This study characterizes the ecology, behaviour and morphology of populations of *Abrocoma schistace*a and *A. uspallata* in north-western Argentina. We carried out live-trapping, tagging and recapture during 2006–2008. Burrow structure and vegetation were described. Diet composition and the activity of chinchilla rats were defined. Both species inhabit rock crevices in the pre-Andean foothills of the Monte Desert. Some of their morphological specializations for saxicolous life, such as foot pads for better traction on rocky surfaces and reduced nails, are convergent with those of other saxicolous species. Both species appear to be diurnal, with activity peaking in the early morning. Dietary analyses suggest trophic specialization by both species. Density of *A. schistacea* was of 0.15 ± 0.06 individuals ha^{-1}; with individuals living in groups of 3–4 animals. Given their low abundance, restricted distribution and high level of habitat and food specialization, we urge that populations of this species be protected through effective management.

Keywords: adaptations; chinchilla rats; Monte Desert; saxicolous species

Introduction

A common habitat for rock-dwelling species consists of isolated accumulations of rocks and boulders that are characterized by a distinctive microclimate as well as a distinctive flora and fauna (scorpions, lizards, bats and rodents; Lacher 1981; Mares and Lacher 1987). Some rodent species that occur only in rock piles in mountainous areas include *Kerodon rupestres*, *Marmota* spp, *Chinchilla lanigera*, *C. brevicaudatus*, *Lagidium peruanum*, *L. viscacia*, *L. wolffsohni*, *Ctenodactylus* sp., *Petromus typicus* and *Petromyscus* sp. (Pearson 1948; Crespo 1963; Armitage and Downhower 1974; Barash 1974; George 1974; Rowlands 1974; Lacher 1981; Mares and Lacher 1987; Arnold 1990; Mares 1997; Galende et al. 1998; Walker et al. 2000a, b; Walker 2001; Coetzee 2002; Parera 2002; Canevari and Fernández Balboa 2003; Galende and Trejo 2003; Walter et al. 2003; Spotorno et al. 2004; Tarifa et al. 2004; Nutt 2005; Rathbun and Rathbun 2006; Werner et al. 2006). These rock-specialist (saxicolous) species experience similar selective pressures and share certain morphological characteristics,

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including shortened tails and reduced toes and nails. These species also possess foot pads, which assist in traction on rock surfaces and protect the feet against impacts (Rowlands 1974; Lacher 1981; Mares and Lacher 1987).

The family Abrocomidae (Rodentia: Hystricognathi) contains two genera, *Abrocoma* with eight species, and *Cuscomys* with one species (Braun and Mares 2002, figure 1). The family is endemic to central western South America, from southern Peru southward to central Argentina (Mares and Ojeda 1982; Braun and Mares 2002; Patterson et al. 2007; Figure 1). *Abrocoma* displays an extremely wide range of variation in morphology, behaviour, distribution, habitat use and natural history (Braun and Mares 2002). *Abrocoma* was described from arid habitats at high elevations (up to 5000 m a.s.l., Redford and Eisenberg 1992; Cortés et al. 2002), where food availability is scarce and distribution of rock piles is heterogeneous (Cortés et al. 2002).

There are six extant species in Argentina, the distributions of which are disjunct (Figure 1). *A. cinerea*, the most thoroughly studied species, is herbivorous and nocturnal (Glanz and Anderson 1990; Cortés et al. 2002), it lives under rocks and in rock crevices and fissures that provide food-hoarding sites and protection (Bárcena and Dacar 1999–2001; Cortés et al. 2002). This species lives in small colonies and probably builds communal latrines (Olrog and Lucero 1980; Redford and Eisenberg 1992; Braun and Mares 1996; Bárcena and Dacar 1999–2001). In contrast, the remaining species of *Abrocoma* are poorly known. For example, based on a single record of an adult female, Thomas (1921) restricted the distribution of *A. schistacea* to southern San Juan Province at Sierra Tontal and Pedernal (Argentina, 2700 m a.s.l.). Glanz and Anderson (1990) later confirmed the presence of this species at Sierra Tontal. Similary, a single individual of *A. uspallata* was captured by Braun and Mares (2002) in the Quebrada de la Vena at Sierras de Uspallata in north-western Mendoza Province (Argentina, 1880 $\pm$ 150 m a.s.l, 32° 39′ 405″ S, 69° 20 970″ W), which represents an unusually arid environment (Braun and Mares 2002).

As this synopsis suggests, few studies have addressed the natural history of the different species of *Abrocoma* for Argentina and Chile (Bárcena and Dacar 1999–2001; Cortés et al. 2002). Thus, the objectives of this study were to characterize habitat, behaviour and morphology of populations of *A. schistace*a (31° 45′ 24″ S, 69° 13′ 28″ W, El Leoncito, San Juan Province, Argentina) and *A. uspallata* (32° 37′ 216″ S, 69° 17′ 93″ W, Uspallata, Mendoza Province, Argentina). In addition to providing new information regarding these aspects of the biology of *A. schistacea* and *A. uspallata*, our data allow comparisons of these species with other saxicolous taxa. In addition to providing a more complete picture of the biology or our study species, our findings will help determine the conservation status of these taxa both of which are endemic to the Monte Desert of the pre-Andean foothills (Diaz and Ojeda 2000).

Materials and methods

Study areas

The study took place at El Leoncito National Park (76,000 ha, 31° 45′ S, 69° 10′ W), in the south-western San Juan Province, Argentina (Márquez 1999). The park includes part of the Monte, Puna and Altoandina phytogeographic provinces in an altitudinal range from 1900 to 4300 m a.s.l (Márquez 1999). A shrubland comprising
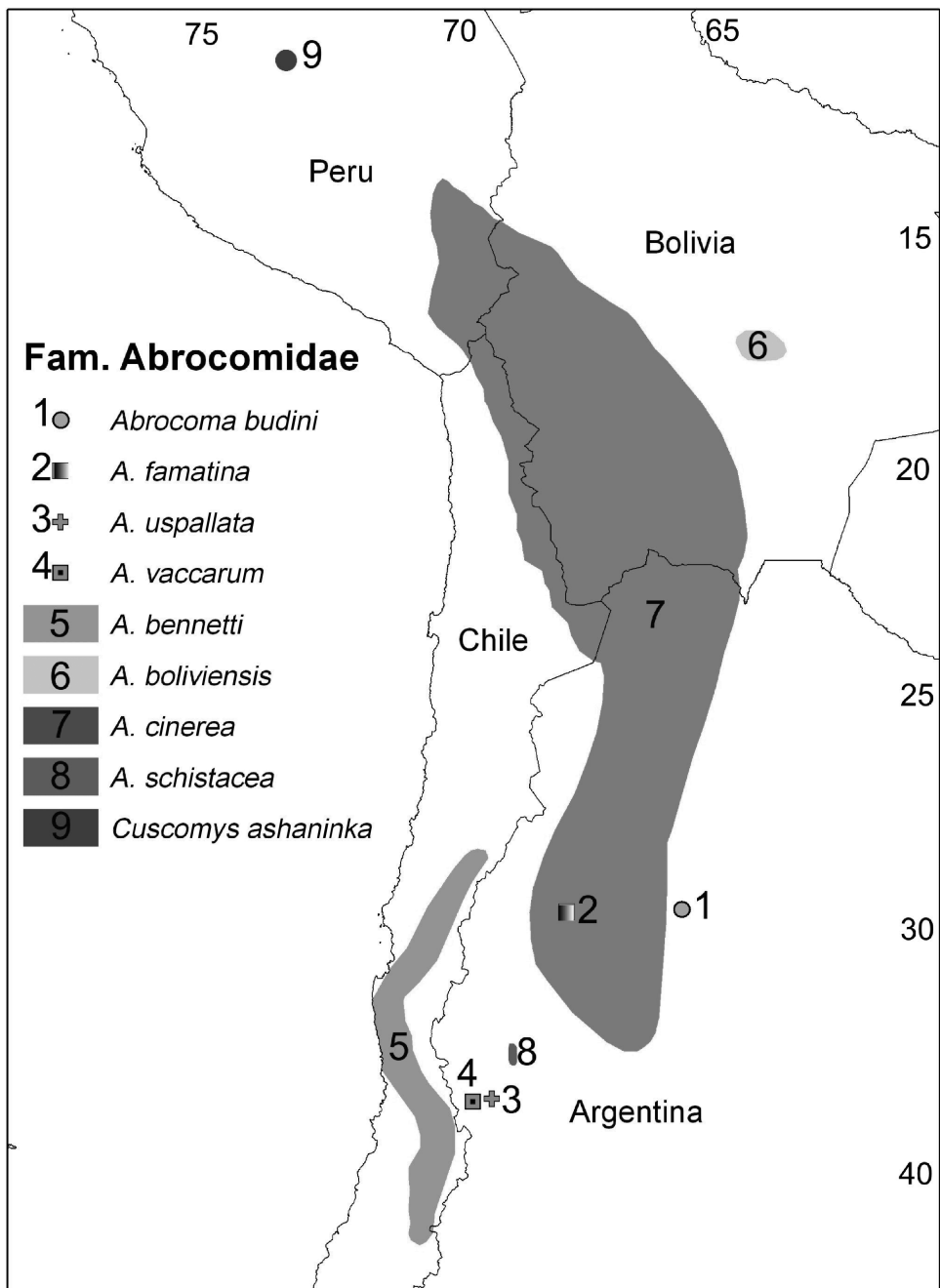
Figure 1. Map of distribution of the different *Abrocoma* species (Patterson *et al*. 2007). Map supplied by M. Tognelli, with permission.

Larrea nitida and *L. divaricata* (dominant shrubs) occurs in ravines, accompanied by a low cover of herbs. The climate in this region is cold and dry with large day/night

and seasonal temperature ranges (mean annual temperature $14.55 \pm 5.65°C$). The predominant winds are from the NW (range of velocity 20–30 km h^{-1} from midday) and are warm and dry. Precipitation occurs as snow or hail in winter (reaching 75 mm), and rainfall in summer (about 25 mm; Le Houérou 1999; Le Houérou et al. 1999). We recorded *A. schistacea* in 13 gulches at an altitudinal range of 2115–2884 m a.s.l, and in latitudinal ranges of 31° 45′ 24.3″–31° 57′ 4″ S, and 69° 13′ 28.5″–69° 22′ 44.4″ W; six sites in each gulch were selected for detailed study.

Sierras de Uspallata (Mendoza Province, Argentina) consists of Monte Desert in the pre-Andean foothills (2072 ± 39 m a.s.l). The climate at this site is transitional between the Andes (characterized by primarily winter precipitations) and lower elevation plains (characterized by primarily summer precipitations; Capitanelli 1969). Mean annual precipitation is 147 mm and mean annual is temperature $10.5 \pm 2.5°C$ (Martínez Carretero and Diblasi, unpublished data); snowfall occurs from July to September. The vegetation consists of grasses (*Stipa*, *Gaillardia*, *Trichocline*) and small shrubs (*Verbena*, *Baccharis*). In the more mountainous areas of the site, a high proportion of soil is bare (Ambrosetti et al. 1986), with the exposed soil being sandy and rocky (Puig et al. 1992). We recorded *A. uspallata* at seven gulches at an altitudinal range of 2060–2136 m a.s.l and within latitudinal ranges of 32° 37′ 216″–32° 37′ 535″ S, and 69° 17′ 93″–69° 18′ 524″ W. We also studied six sites in each gulch.

Description of burrows

All active burrows were identified based on evidence of recent activity such as mounds of fresh faeces near rock crevices. For each active burrow system, the breadth, height (from the foot of the ravine), orientation and depth of the rocky crevices used as burrow entrances were recorded. Burrow location, type of soil and vegetation were described.

Vegetation sampling

Plant resources in each gulch were quantified along nine transects, using the strip transect method, with each strip divided into rectangular segments (Braun 1973). Sampling units were determined by the minimum area method (Matteucci and Colma 1982). All plant species present, their abundance and percent cover were recorded for all grasses and shrubs. We determined the diversity of resource availability in the habitat using the Shannon Diversity Index (H′).

Population and group characterization

Animals were live-trapped using Tomahawk traps ($15 \times 15 \times 60$ cm; Tomahawk live trap No 202/203, Tomahawk, USA) baited with apples, oats and vanilla extract. At each site, trapping was conducted over 7–13 consecutive days. Traps were set near all crevices at which chinchilla rat activity had been detected. At El Leoncito, individuals were captured during the autumn (2006 and 2007), summer (2007 and 2008), and spring (2006 and 2007). At Uspallata, individuals were trapped in summer (2008).

Morphological characteristics

Upon first capture, each individual was marked by attaching a uniquely numbered metal ear tag ($0.6 \times 0.2 \times 0.05$ cm; National Band and Tag Co. Newport, USA) to one ear pinna. Sex, age, body mass, total body length, skull length, hind-foot length, and pinna length were recorded for each individual. Pelage and incisor colouration, number of foot pads and nail development were described. A photograph was taken of each captured animal.

Records of activity

At El Leoncito, the soil near latrines and next to vegetation was smoothed or covered with a fine layer of sand to provide a fresh substrate for monitoring animal activity via footprints; 17 such sites were monitored. Each footprint trap was checked early in the morning, in the afternoon, at sunset and hourly during the night; after each check the sand was again smoothed to provide a fresh substrate. Monitoring continued for three days, after which any sand added to these sites was removed. In addition, camera traps were used to determine whether the study species are diurnal or nocturnal. Four film-based camera traps (Cannon Prima AF-9s Date, Cannon lens 35 mm) and two digital camera traps (Cuddeback NoFlash Infrared Digital Camera System) were used. The cameras were installed at capture sites for *Abrocoma* and near crevices at which evidence of chinchilla rat activity was greatest. Camera traps were deployed for one year (2007), during which they were checked periodically to insure that they were functioning properly. Neither type of camera traps could be used at Uspallata because extensive human activity created concerns regarding camera security.

Diet determination

Microhistological analyses were conducted to determine diet composition for both study species. Fresh faeces were collected from near burrow entrances used by *A. schistacea* ($N = 12$ samples) and *A. uspallata* ($N = 5$ samples). Plant remains present in faeces and reference preparations (from vegetation samples collected at the study site) were processed following the technique of Dacar and Giannoni (2001), which is based on observation of epidermal remnants of leaves, seed and stem cuticles. The abundance of each plant species detected in the faecal samples was expressed as a percentage of that species' frequency. We estimated trophic niche breadth for each study species using the Proportional Similarity Index (PS; Feinsinger et al. 1981).

Statistical analysis

Total plant cover at each study site was compared with a t-test. Seasonal differences in plant cover at each site were examined using one-way ANOVAs. Differences in trophic niche breadth among seasons and differences in the Proportional Similarity Index between sites were also examined using one-way ANOVAs. Interspecific differences in morphological measurements were assessed using Kruskal Wallis test. χ^2 (chi-squared) tests were used to compare the abundance of plant species in the habitat versus in faecal samples from *A. schistacea* and *A. uspallata*; with Pearson Residuals (r (Pearson Residuals) $= f$ (frequency) observed $- f$ expected

/ $\sqrt{f}$ expected) used to quantify the relative abundance of plant species in each dataset. One-way ANOVAs were used to compare characteristics of burrows at both sites; for those analyses yielding a significant result, post-hoc tests Tukey test ($p < 0.05$) were then used to identify the specific sites contributing to this outcome. Results are expressed as sample mean ± standard error. Circular statistics were used to determine whether the distribution of active holes in burrow systems at each site was at random (Rayleigh test).

Results

Description of burrows

Both study species inhabited crevices in rock piles. However, the burrows of *A. schistacea* were on a hillside with rocky flagstone walls while those of *A. uspallata* were on hillsides composed of rock blocks or flagstones that crumble easily.

Burrow system attributes for both study sites are summarized in Table 1. Crevices were significantly larger (diameter: F = 8.22; *df* = 1; *p* = 0.005) and galleries were significantly deeper (F = 6; *df* = 1; *p* = 0.017; Table 1) at Uspallata than at El Leoncito. Crevices were also at significantly higher elevation at Uspallata (F = 31.92; df = 1; *p* < 0.0001; Table 1). The number of holes per burrow system was significantly smaller at Uspallata (*T* = 2.81; df = 2; *p* = 0.006; Table 1), although the distance between burrows was significantly greater at this site (T = −2.25; df = 13; *p* = 0.042; Table 1). At El Leoncito, the plant species located nearest to burrows were shrubs such as *Gymnophyton sp*. (cover 27.6%) and *Larrea sp*. (cover 20.7%). In contrast, plant species located nearest to burrows at Uspallata were herbs such as *Stipa sp.* (cover 23.3%), shrubs such as *Larrea divaricata* and *Atriplex lampa*, and cacti (cover 13.3%).

At El Leoncito, the crevices containing burrows were located on the east-facing hillsides, where they received morning sunlight. The orientation of burrow holes was most frequently north-easterly–easterly (mean angle of orientation 81° 30′ ± 0° 05′; Rayleigh test of uniformity *p* = 0.0001). At Uspallata, the majority of crevices were on south-west-facing hillsides, where they received afternoon sun. Burrow holes were homogeneously distributed, with no predominant orientation (mean angle of orientation 348° 69′ ± 53° 55′, Rayleigh test of uniformity *p* = 0.57).

Table 1. Burrow system characteristics at El Leoncito and Uspallata. Mean ± standard error. * indicates significant differences (*p* < 0.05).

Sites	Number of holes per burrow	Diameter of crevices (cm)	Depth of galleries (cm)	Height of crevices from foot of hill (m)	Distance between burrows (m)	Soil on hillsides	Distance to the nearest vegetation (m)
El Leoncito	5.4 ± 0.5	8.4 ± 0.9	29.5 ± 3.5	5.8 ± 0.5	127.4 ± 49.9	Flagstones	3.7 ± 0.4
Uspallata	3.4 ± 0.7*	12.3 ± 1.4*	43.7 ± 6.8*	11.1 ± 0.9*	321.5 ± 24*	Rock blocks or flagstones	2.9 ± 0.4

Vegetation sampling

At both sites, the shrubs and herbs occurring in ravines were heterogeneously distributed across slopes; this distribution appeared to be due largely to the irregular occurrence of rock outcrops at each site. During the summer (the only season during which samples were collected from Uspallata), total plant cover was significantly greater at Uspallata (T = −4.75; $p < 0.0001$; df = 97). At Uspallata, total plant cover in summer was 37.15 ± 3.73% and species richness was 25 plant species. At El Leoncito, total plant cover in summer was 14.92 ± 2.83%, with plant species richness being 11 species.

When all data for El Leoncito were pooled, total plant cover was 23.31 ± 1.81%. There were significant differences in plant cover among seasons (F = 6.51; df = 2; $p = 0.002$; N = 126). Plant cover was lower in summer (January 2007, 14.92 ± 2.83%) than in autumn (April 2006; 27.62 ± 2.85%) or spring (October 2006; 28.42 ± 3.42%). Species richness was higher in autumn (15 plant species) with more herbs than in other seasons of the year (spring: 10 plant species; summer: 11 plant species). There were no differences in shrub cover across seasons (F = 0.27; $p = 0.77$; df = 2; N = 160), but herb cover was lower in summer (2.32 ± 0.65%) than in autumn 6.63 ± 1.09%. Shrubs provided a significantly higher percentage of ground cover (15.8 ± 1.26%; F = 16.9; $p < 0.0001$; df = 2; N = 242) compared to herbs (5.41 ± 0.66%) and cacti (1.25 ± 0.75%). The dominant vegetation consisted of *Gymnophyton polycephalim* (27.6%), *Larrea nitida* and *L. divaricata* (20.7%).

At Uspallata, the 14 shrub species identified provided 12.08 ± 2.82% of total plant cover. In contrast, the 10 herb species identified provided 3.78 ± 2.65% of total ground cover and the one cactus species identified provided 1.09 ± 0% of total ground cover. Shrubs provided the habitat with more ground cover than herbs (F = 9.14; $p = 0.001$; df = 2; N = 25). Dominant shrubs included *Bulnesia retama* (40%), *Larrea divaricata* (24%) and *L. cuneifolia* (20%), and the dominant herb was *Atriplex undulata* (27.3%).

Population and group characterization

Density of *A. schistacea* was 0.15 ± 0.06 individuals ha^{-1}. Individuals live in groups of 3–4 individuals; the groups captured consisted of one male and two females or two males and two females (N = 3 groups). Data regarding density and group structure were not obtained from Uspallata as only one chinchilla rat was captured. Members of both species used readily identifiable latrine sites that comprised piles of faecal pellets. Fresh faeces were blackish brown and shiny; the resulting latrines were black or reddish and sometimes had a crystalline appearance due to the deposition of urine at these sites.

Morphological characteristics

Dorsal colouration of *A. schistacea* is a drab grey, with slightly darker pelage along the midline. Hairs of the venter are greyish for most of their length; overall, ventral colouration is similar to but somewhat paler than the dorsum. The dorsal surface of the tail is like the midline of the dorsum; the underside of the tail is white. The fore and hind feet are covered with whitish hairs. The dorsal colouration of *A. uspallata* is greyish brown and the venter is washed with white. The dorsal surface of the tail is

Table 2. Morphologic traits of *A. schistacea* and *A. uspallata*. Body measurements of our *A. uspallata* sample were supplemented with those recorded by Braun and Mares (2002) and those of one individual of the IADIZA collection (Mendoza, Argentina). Mean ± standard error. Number of individuals is between brackets. * indicates significant differences ($p < 0.05$).

Traits	*A. schistacea*	*A. uspallata*
Body mass (g)	174.1 ± 10.1 (9)	157.3 ± 16.8 (3)
Body length (mm)	161.6 ± 2.1 (9)	175.3 ± 11.5 (3)
Tail length (mm)	101.3 ± 2.6 (10)	118.7 ± 6.4 (3)*
Total length (mm)	263.6 ± 4.1 (9)	294 ± 15.8 (3)*
Skull length (mm)	52.2 ± 1.9 (10)	49.3 ± 6.8 (2)
Hindfoot length (mm)	27.9 ± 0.6 (10)	29.2 ± 1.0 (3)
Pinna length (mm)	25.6 ± 1.2 (10)	28.3 ± 2 (3)
Tail/body length %	63.1 ± 1.6 (9)	68.1 ± 4.3 (3)
Tail/total length %	38.6 ± 0.6 (9)	40.4 ± 1.5 (3)

also greyish brown and the underside of the tail is white. In both species, the sternal gland is covered with hairs that are white to the base. The fore and hind feet of both species have foot pads and both species have reduced nails. *A. schistacea* has buccal epidermal denticles or false teeth, in the midline of the mouth, and a tongue with a horny pad. The larger, anteriorly positioned tooth appears to be bilobed and directed posteriorly. These traits were not examined in *A. uspallata*.

Ten chinchilla rats were captured at El Leoncito, but only one at Uspallata. Our body measurements for this sample were supplemented with those obtained by Braun and Mares (2002) for *A. uspallata* from Quebrada de la Vena at Sierras de Uspallata and with those of one individual housed in the IADIZA collection (Table 2). Based on this data set, no significant differences were found between species for mass, total length, skull length, hindfoot length, or pinna length (Table 2). Similarly, percentages of tail/body length and tail/total length did not differ between the study species (Table 2). In contrast, there were significant differences in tail length (H = 4.46; $p = 0.035$; df = 1) and total length (H = 4.52; $p = 0.036$; df = 1), with both measurements being larger for *A. uspallata*. For *A. schistacea*, sexual dimorphism (calculated as male body mass/female body mass) was 1.03; suggesting that in this species the sexes do not differ with respect to body mass.

Records of activity

The camera traps did not record any chinchilla rats. We recorded 15 footprints and two tail prints of *A. schistacea* very early in the morning (before 8–10 am). Camera and footprint traps were not used to monitor *A. uspallata*; members of this species were captured between 9 and 11 am. Although preliminary, these data suggest that both species are active during the daytime, with activity apparently being most pronounced during the morning.

Diet determination

For *A. schistacea*, the diversity of food available was greater in autumn than in summer (t = 3.628; df = 29; $p = 0.001$, Ha′ = 2.955; Hs′ = 2.245) although trophic niche

breadth was narrower in autumn (F = 1480.87; $p < 0.0001$; df = 1; N = 24; 0.29 ± 0.01 PSa (Proportional Similarity Index in autumn) 0.61 ± 0.01 PSs (Proportional Similarity Index in summer)). The reverse occurred in summer. There were significant differences between the per cent availability of plants and the per cent plant composition of the diet of this species ($\chi^2 = 39.43$; $p < 0.0001$; df = 5). In particular, *Gymnophyton*, *Stipa* and *Bougainvillea* appeared to be avoided by this chinchilla rat, with these species representing 0% of the diet but 6.6 ± 3.2%, 2.4 ± 1.6% and 1.5 ± 0.2% (respectively) of the vegetation in the habitat. In contrast the percentage of *Lycium* in the diet was 6.8 ± 1.1% versus 1.1 ± 0.8% in the habitat. In both autumn and summer, *Larrea* sp. exceeded 80% of diet but represented only 8.1 ± 0.8% of the vegetation available for consumption, suggesting that *A. schistacea* is a dietary specialist.

Significant differences between diet composition and plant availability were also found for *A. uspallata* ($\chi^2 = 33.22$; $p < 0.0001$; df = 8). In particular, the occurrence of *Lycium* and *Schinus* sp. in the habitat was lower (3 ± 0% and 0.01 ± 0% respectively) than the occurrence of these taxa in the diet (34.2 ± 8.3% and 24 ± 7.3% respectively), suggesting that these species were preferred diet items. While *Larrea* sp. formed the large majority of the diet of *A. schistacea*, *Larrea* sp. represented only 30 ± 5.9% of the diet of *A. uspallata*.

There were significant differences between study sites with respect to Proportional Similarity Index (F = 25.53; $p < 0.0001$; df = 1; N = 16). In the summer, trophic niche breadth was wider at El Leoncito (PS = 0.61 ± 0.01) than at Uspallata (PS = 0.42 ± 0.06). These findings are supported by our observations of the range of items consumed by each species. For example, while the diet of *A. uspallata* contained 3.2% arthropods and 1.6% shrub roots, neither of these items were found in the diet of *A. schistacea*.

Discussion

The natural histories of the six species of *Abrocoma* that occur in Argentina are generally similar although the mountain habitats in which these species occur are disjunct and often completely isolated from other mountainous areas (Braun and Mares 2002). The *A. cinerea* complex is generally highly specialized for life on rocky cliff faces, and members of this complex display many adaptations for a saxicolous existence (Braun and Mares 1996; Mares 1997), including structural specializations of the feet. While *A. cinerea* could be characterized as an altiplano specialist that includes rocks within its preferred microhabitats (Braun and Mares 2002), our study species appear to be more specialized for life in rocky areas. For example, rock crevices inhabited by *A. uspallata* and *A. schistacea* are largely inaccessible to other animals, and the crystalline faecal and urine piles (middens) present near crevices suggest long use and fidelity of chinchilla rats to particular crevices (Braun and Mares 2002). Rocks also provide the only reliable refuge from predators, serve as lookout posts for predator detection, and provide sites for hibernation and successful rearing of young (Mares and Lacher 1987). In these ways, crevices appear to serve functions similar to those reported for other rock-dwelling rodents such as *Ctenodactylus gundi* (Ctenodactylidae; George 1974). Collectively, these observations suggest that our study species are habitat specialists that are unlikely to be found in areas lacking rocks (Braun and Mares 2002).

Saxicolous species occupying similar habitats display remarkable convergences in morphology and ecology. For example, saxicolous species generally defaecate on piles of boulders, are herbivorous, use alarm whistles, have small litters of precocial young, defend individual boulder piles and show harem polygyny (Mares and Lacher 1987). Morphologically, these animals have rather long snouts, leather-like pads on the feet, and lack a tail (Mares and Lacher 1987). Consistent with other rock-dwelling taxa, chinchilla rats have many adaptations for a saxicolous life. Their specializations include padded feet with leathery tubercles on the pads. Similar structural modifications of the feet have been reported for the rock-dwelling lagomorphs *Pronolagus* (Leporidae) and *Ochotona* (Ochotonidae), as well as the woodrat *Neotoma cinerea* (Muridae, Rodentia), the feet of which are heavily padded with hair. Similarly, the mountain vizcacha (*Lagidium* sp., Chinchillidae) has fleshy pads or pallipes on the soles of the feet. Such projections are thought to improve the grip of the feet on unstable or crumbling rocks (Rowlands 1974). Specialized padding on the feet is apparently associated with reduction of the claws; 73% of the animals that have padded feet also have small and/or blunt claws (Mares and Lacher 1987).

Another saxicolous characteristic of *A. vaccarum* (Braun and Mares 1996), *A. bennetti* (Mann 1978), *A. schistacea* and *A. uspallata* that may reflect a saxicolous lifestyle is that these species make massive latrines on rock piles. These latrines are made up of faeces and are held together with thick urine. Latrines are either black or reddish-brown, and may have a crystalline or even an epoxy-like feel. These deposits have a strong odour and can be used to locate individuals and colonies. *A. schistacea*, *A. cinerea* (Mann 1978) and *A. vaccarum* (Braun and Mares 1996) live in small colonies and we suggest that these massive latrines correspond to a colony of animals (Braun and Mares 1996). With regard to daily activity, *A. schistacea* and *A. uspallata* appear to be diurnal, with activity peaking early in the morning. In contrast, Braun and Mares (1996) suggested that *A. vaccarum* is active at night, with activity continuing into the early morning. The challenges associated with living in isolated rock piles likely impose shared selective pressures on mammals that attempt to exploit these habitats, with the result that similar adaptations are required for successful colonization of these habitats (Mares and Lacher 1987).

A. uspallata and *A. schistacea* occur in Monte Desert habitat (Precordillera) characterized by arid-adapted shrubs, cacti (Braun and Mares 2002) and herbs. Both species occupy rocky crevices located on slopes composed of flagstones or massive stone blocks. Similarly, *A. vaccarum* and *A. cinerea* are restricted to rocky cliff faces, occurring either at the base of a slope or in fissures that open high up in a rock wall (Braun and Mares 1996). *A. famatina* in La Rioja Province and *A. budini* in Catamarca Province live under rocks and in rock crevices or fissures (Thomas 1920a, b). Despite the generally similar habitats occupied by these species of *Abrocoma*, differences in burrow structure are evident between species. For example, at our study sites at Uspallata, burrows were bigger and deeper and were located at higher elevations than at El Leoncito. Further, while the majority of burrows at El Leoncito (San Juan) were located on NE–E facing slopes (receiving morning sun) most burrows at Uspallata (Mendoza) were located on SW facing hillsides (receiving afternoon sun). Thus, within the general framework of convergence for saxicolous life, variation is evident and may reflect adaptation to local variation in rocky habitats.

The high percentage of *Larrea* in the diet of *A. schistacea* suggests that this species is a dietary specialist. During the summer, trophic niche breadth was wider at El

Leoncito than at Uspallata. Our data suggest a difference in feeding habits between the study species. Although *A. schistacea* appears to be more specialized with regard to diet, this is probably due to a comparatively limited availability of trophic resources. The Proportional Similarity Index for *A. schistacea* was greater than that for *A. uspallata*, providing apparent support for the hypothesis that the former species follows an opportunistic foraging strategy. In contrast, *A. uspallata* included more species in its diet and consumed species in proportions that differed from their representation in the habitat, suggesting a more selective foraging strategy that may have been related to the higher plant cover and diversity present at Uspallata. With regard to seasonal variation at El Leoncito, as well as variation between the study sites, our data concur with expected relationships in that the lower the availability of resources, the wider the breadth of the trophic niche (Feinsinger et al. 1981). Published data indicate that *A. vaccarum* also eats leaves and stems of *L. divaricata* (Braun and Mares 1996). In contrast, *A. cinerea*, in Peru, feeds on the stem and flowers of *Lepidophyllum quadrangulare* and *Ephedra*, and leaves of *Polylepis trea* and *Azorella compacta* (Braun and Mares 1996). Based on these comparative data, we suggest that *A. schistacea* and *A. vaccarum* (Braun and Mares 1996) are *Larrea* specialists. The ability to digest *Larrea*, with its many tannins and resins (Mabry et al. 1977), is rare among mammals and suggests that these species may also display physiological specializations associated with their reliance on this food resource.

An adaptation for manipulating food is the occurrence of buccal modifications for grasping or masticating food. *A. schistacea* and *A. vaccarum* have buccal epidermal denticles or false teeth along the midline of the mouth and a tongue with a horny pad (Braun and Mares 1996). These buccal teeth are not preserved with the skull or other skeletal material, but appear to be epidermally derived denticles that function as additional midline teeth (Braun and Mares 1996). The larger, anteriorly positioned buccal tooth appears to be bilobed and directed posteriorly. The function of this anterior tooth seems to be to maintain food items on the tongue and to push them forward against the rough palatal ridges and molariform teeth. The function of the posterior tooth seems to be to manipulate food inside the mouth (Braun and Mares 1996). Both teeth form a barrier to the forward movement of food in the mouth. These teeth were not found in any of the specimens examined by Braun and Mares (1996), indicating that they are not preserved in skulls that have been cleaned and are likely derived from soft tissue rather than bone.

Conservation threats to our study species have not been described and these taxa are listed as data deficient on the IUCN Red List. The Administration of National Parks places special value on *A. schistacea* because this species is endemic to El Leoncito National Park and the adjacent region. Concerning rarity, both species are characterized by low numbers of individuals, a restricted geographic distribution and high degree of habitat specialization. Given these attributes, populations of these species should be protected. The systematics of the genus *Abrocoma* are poorly known (Braun and Mares 2002). The fact that various members of the *cinerea* complex appear to be confined to isolated patches of rocky habitats along the Precordillera and Sierras Pampeanas mountains of the eastern Andes suggests a classic pattern of allopatric speciation. Because of their specialization for rocky habitats in isolated mountain areas, speciation along the Andes seems likely to have occurred (Braun and Mares 2002). Collectively, these traits suggest that *Abrocoma* is an ideal taxon in which to examine adaptation, speciation and differentiation. By using molecular techniques, it should

be possible to discern phylogenetic relationships among species and to estimate the timing of colonization and speciation events and to relate these historical occurrences to orographic and climatological events in the Andes (Braun and Mares 2002).

Acknowledgements

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